

A SURVEY OF *SOLANUM* PRICKLES AND MARSUPIAL HERBIVORY IN AUSTRALIA¹

D. E. SYMON²

ABSTRACT

A survey of the prickliness of *Solanum* in Australia is made and the distribution of the most prickly species is mapped. A survey of the diets of vertebrate herbivores in Australia is presented. It is concluded that the development of prickles is not a response to the physical environment but to browsing by marsupials belonging primarily to the group known as wallabies.

It is commonly asserted (Kerner, 1897; Fritsch & Salisbury, 1953; Davis & Heywood, 1967) that prickles are an adaptation to arid environments or to heavy grazing. If the second assertion is correct, one could expect to find some spacial relationship between the presence of herbivores and the distribution of prickly species. A survey of a large genus displaying varied prickliness over a substantial area may be a way of showing any relationship and is attempted here. The availability of a recent revision of *Solanum* in Australia in which data on the species and their distribution are available (Symon, 1981) enables such a comparison to be made. The genus *Solanum* is not unique in its varied prickliness and occurrence over large parts of Australia; other large genera that might also be surveyed are *Acacia* or *Hakea* but both of these lack comprehensive revisions.

Familiarity with *Solanum* in Australia has lead me to doubt any special relationship between prickles and aridity and a glance at Figure 1 does not indicate any special concentration of prickliness in the most arid areas nor is this supported in Table 2, which shows the distribution of prickly species in relation to moisture index. This aspect will not be followed further here.

The survey is presented in three sections. First, an estimate of prickliness was determined for all species of *Solanum* in Australia and the distribution of the most prickly species was mapped. Second, an extensive survey of the reported diets of herbivores was made in an attempt to discover what animals were significant herbivores and exactly what they ate. An appalling lack of knowledge of diets was revealed but all principal her-

bivores are discussed in detail. Third, a brief survey is made of exotic *Solanum* species on some islands where vertebrate herbivores are absent.

Two sections of the genus native to Australia are completely unarmed, sect. *Solanum* (Black nightshades) and sect. *Archaeosolanum* (Kangaroo apples). The species are small or large shrubs growing mostly well within the range of herbivores. An alternative strategy of plant protection must be operating and in this regard it is notable that the level of alkaloids in these two sections is considerably higher than in the sections with prickly species (Bradley et al., 1978).

MATERIALS AND METHODS

A measure of prickliness for each native *Solanum* species was obtained by counting the number of prickles on 4 cm lengths of stem on herbarium specimens. At least 10 collections of each species were examined (or all that were available in rare species). The lengths of about 50 prickles were measured for each species. Old weathered stems were excluded and where possible a distinction was made between those specimens in juvenile phases of growth and mature specimens. However, few herbarium specimens contain information on the age of the shrub, position of the sample, or details of prickle distribution on the plant.

RESULTS

A total of 83 species was examined (Table 1). Two species were so inadequately represented that no worthwhile estimate was made; *S. ca-*

¹ I am particularly grateful to P. B. Copley and A. C. Robinson for allowing me access to unpublished data on the diet and distribution of *Petrogale xanthopus*, to the latter for advice and assistance on the distribution of many species of marsupials, and to Dr. G. D. Sanson for helping to sort out the browsers and grazers. This paper was part of the Second International Symposium of the Biology and Systematics of the Solanaceae presented at the Missouri Botanical Garden on 3–6 August 1982.

² Botanic Garden, North Terrace, Adelaide, South Australia, 5000.

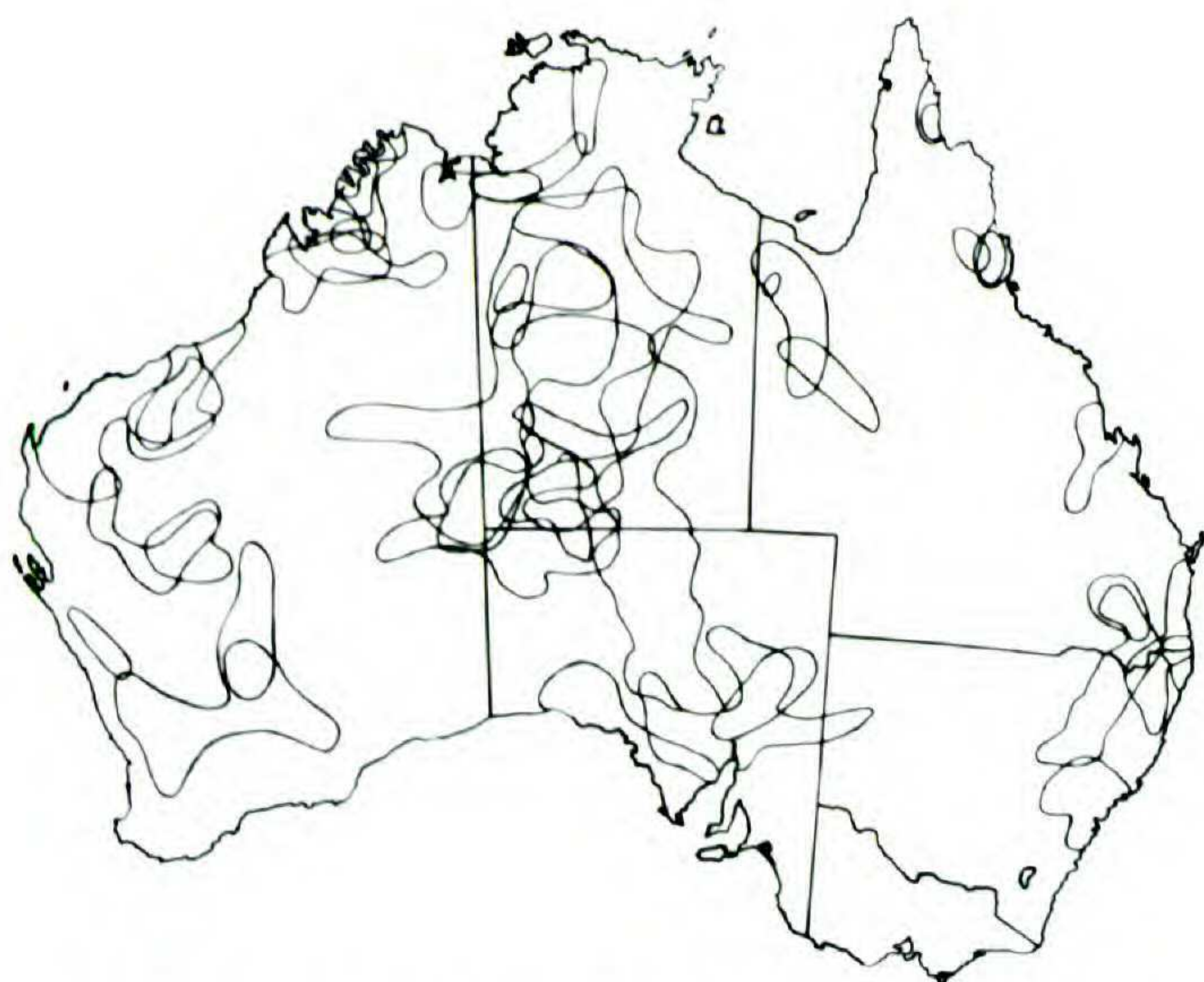


FIGURE 1. Distribution of the most prickly species of *Solanum*.

taphractum A. M. Cunn. ex Benth. from the north west coast of Western Australia and *S. sporadotrichum* F. Muell. from the Queensland rainforest, and these two will not be discussed further. Six species were unarmed in the specimens available. No prickles were found on *S. densevestitum* F. Muell., *S. nemophilum* F. Muell., or *S. tetrandum* R. Br., and these three are believed to be wholly unarmed. The few specimens of *S. dunalianum* Gaudich that were available were unarmed but it is known from specimens from New Guinea that this species has the potential to produce prickles and a range of juvenile plants and more collections are needed to get any estimate of prickliness. This species is restricted in its distribution in Australia to the far north of Cape York. *Solanum viridifolium* Dunal is a small tree found in the rainforests of Queensland and is unarmed in the many herbarium sheets available. Young plants collected by B. Hyland at Atherton, and plants grown from seed, have sparse weak prickles on the main stem in the juvenile phase and the taxon certainly has the potential to produce prickles although it is completely unarmed when mature. *Solanum tumulicola* Symon is an herbaceous perennial found about Daly Waters in the Northern Territory. It is unarmed in most collections, but a few plants do have some small weak prickles towards the base and, like *S. viridifolium*, the species has the capacity to produce prickles. All other species can be described as prickly to a greater or lesser extent. The lower level of prickliness is represented by *S. esuriale* Lindley, 10 collections from each of Western Australia, Northern Territory, and Queensland had no prickles whereas collec-

tions from New South Wales and South Australia averaged about one prickle per 4 cm length. At the other extreme are *S. semiarmatum* F. Muell. from eastern Australia with a mean of 70 prickles per 4 cm length of stem and *S. ashbyae* Symon from Western Australia with 43 prickles.

Several species are conspicuously prickly on the main stem in the juvenile phases of growth and have fewer prickles on mature and distal twigs. Few herbarium specimens represent such species adequately and more may show this characteristic than have been recorded. Conspicuous examples are: *S. inaequilaterum* Domin, 37 below, six above; *S. macoorai* Bailey, 26 below, five above; *S. asymmetriphyllum* Specht, six below, 0.3 above; *S. clarkiae* Symon, 39 below, 21 above. The first two are found in the rainforest of eastern Australia and the second two at the foot of the escarpments in northern Arnhemland. All but *S. clarkiae* will form small treelets, and if the prickles do deter herbivores it is an attractive guess that the later, lightly armed leaves and twigs are out of reach.

In almost all species the stems are more strongly armed than the leaves. No count of prickles per unit leaf area has been made, but *S. lacunarium* from the Darling-Murray river system and with an inland population near Lyndhurst in South Australia has leaves that are more prickly than the stems. Two possible reasons for this difference between stems and leaves may be suggested. Leaves may be more expendable than stems because a leaf once lost may be replaced by a new one but the loss of a stem is more serious damage. Secondly, to be effective prickles are best held rigidly, and flaccid leaves may not be fully effective bases for prickles. In most cases prickles on leaves are concentrated on the stronger main veins and lower portions of the leaf. If leaves are bitten as a mouthful, relatively few prickles may be effective. Little is known of what animals graze *Solanum*, but judged by human impressions many leaves seem ineffectively protected and one would expect a fastidious small grazer to be able to nibble such leaves with relative ease. Although it is true that some degree of prickliness would deter vertebrate herbivores, many species are so lightly armed that the effectiveness of their prickles can be seriously questioned.

Contemporary accounts of the effectiveness of prickles seem to be very sparse. Janzen (1981), in a review of legume defences against herbivores, only mentioned prickles in discussing the

TABLE 1. Prickliness of Australian *Solanum* species. Mean number per 4 cm length of stem and mean length (mm).

	No.	Length (mm)
<i>adenophorum</i>	6.3	3.9
<i>ashbyae</i>	43.3	5.2
<i>asymmetriphyllum</i> young	6	4.4
old	0.3	3.3
<i>beaugleholei</i>	24.7	5.0
<i>brownii</i>	4.0	6.0
<i>campanulatum</i>	16.4	4.4
<i>carduiforme</i>	22.3	4.3
<i>centrale</i>	2.0	3.0
<i>chenopodium</i>	1.5	6.3
<i>chippendalei</i>	14.5	4.1
<i>cinereum</i>	10.0	7.6
<i>clarkiae</i> young	39.5	4.8
old	21.0	4.0
<i>cleistogamum</i> W.A.	18.0	4.9
N.T.	16.0	3.1
<i>coactiliferum</i> W.A.	3.7	3.8
N.T.	2.2	4.1
N.S.W.	2.4	3.6
east S.A.	4.3	4.4
west S.A.	2.1	4.0
<i>cookii</i>	16.6	5.6
<i>corifolium</i>	1.4	5.0
<i>cunninghamii</i>	8.6	2.8
<i>dallachii</i>	0.7	4.6
<i>densevestitum</i>	0	0
<i>dianthophorum</i>	13.7	4.3
<i>dimorphispinum</i>	3.0	4.6
<i>dioicum</i> King Leopold	8.5	3.1
Gibb & Hann R.	4.0	3.8
Tanami Desert	18.4	5.3
<i>discolor</i>	4.8	5.0
<i>diversiflorum</i>	4.4	6.0
<i>dunalianum</i>	0	0
<i>eardleyae</i>	33.9	4.9
<i>eburneum</i>	15.9	4.1
<i>echinatum</i>	9.5	3.5
<i>elachophyllum</i>	4.0	10.5
<i>elegans</i>	2.6	5.9
<i>ellipticum</i> typical	11.8	4.4
NT prickly	29.3	6.8
SW Eyre Pen.	7.8	4.6
<i>eremophilum</i>	8.3	4.2
<i>esuriale</i> W.A.	0	0
N.T.	0	0
Q.	trace	
N.S.W.	1.1	2.4
S.A.	0.7	2.5
<i>ferocissimum</i> N.T.	4.1	4.5
Q.	4.0	6.1
N.S.W.	5.2	5.7
<i>furfuraceum</i>	1.4	7.6
<i>gabrielae</i>	3.7	4.0

TABLE 1. Continued.

	No.	Length (mm)
<i>gilesii</i>	6.3	4.8
<i>hamulosum</i>	6.7	3.6
<i>hesperium</i>	4.3	1.6
<i>heteropodium</i>	32.8	4.2
<i>hoplopetalum</i>	24.5	5.2
<i>horridum</i>	40.2	4.9
<i>hystrix</i>	17.1	4.3
<i>inaequilaterum</i> young	37.4	5.9
old	6.5	4.8
<i>karsensis</i>	1.6	7.8
<i>lachnophyllum</i>	38.2	4.5
<i>lacunarium</i> inland	2.1	2.1
main river	3.5	2.3
<i>lasiocarpum</i> (ferox)	15.1	3.0
<i>lasiophyllum</i> (Giles)	24.1	4.9
W.A.	16.7	3.2
<i>leopoldensis</i>	16.3	4.3
<i>lucani</i> W.A.	18.8	3.8
N.T.	23.7	4.5
<i>macoorai</i> young	26.1	6.6
old	5.3	4.1
<i>melanospermum</i> young	16.0	—
old	4.0	—
<i>multiglochidiatum</i>	27.0	3.75
<i>nemophilum</i>	0	
<i>nummularium</i>	3.7	6.7
<i>oedipus</i>	40.5	7.0
<i>oldfieldii</i>	3.3	3.5
<i>oligacanthum</i>	4.0	5.6
<i>orbiculatum</i> ssp. orbic	2.0	6.4
ssp. macro	1.9	7.3
<i>papaverifolium</i>	14.1	3.4
<i>parvifolium</i>	4.7	4.7
<i>petraeum</i>	23.4	3.2
<i>petrophilum</i> (Flinders)	12.5	6.4
<i>phlomoides</i>	19.1	4.3
<i>plicatile</i>	3.4	2.8
<i>prinophyllum</i>	9.1	7.8
<i>puguinculiferum</i>	2.7	9.2
<i>pungetium</i>	3.5	4.8
<i>quadriloculatum</i>	18.0	3.9
<i>seitheae</i>	21.5	3.7
<i>semiarmatum</i>	70.1	3.1
<i>sporadotrichum</i> (1)	26.0	4.4
<i>stelligerum</i>	1.5	5.3
<i>sturtianum</i> W.A.	1.3	3.3
S.A.	0.8	3.3
<i>terraneum</i>	3.3	2.4
<i>tetrandrum</i>	0	
<i>tetrathecum</i>	1.2	7.6
<i>tudununggae</i>	1.2	2.6
<i>tumulicola</i>	0	
<i>vansittarensis</i>	0.7	5.8
<i>viridifolium</i>	0	
<i>yirrkalensis</i>	2.8	3.5

ant-thorn *Acacia*. There is no mention of conventional prickles, thorns, pungent leaves, or vertebrate herbivores. Main (1981), in discussing plant responses to herbivory, mentioned nutritional value and toxicity but not tomentum or prickles. Tomlinson (1962), in discussing the prickles of palms, did consider that they are a response to herbivory and gave some interesting information on their origin and distribution.

A SURVEY OF THE PUBLISHED DATA ON THE DIETS OF HERBIVORES IN AUSTRALIA

INSECTS

No adequate survey of insect herbivores on *Solanum* is available. Many leaves bear evidence of insect activity. I have observed that flea beetles (Fam. Chrysomelidae), looper caterpillars (Fam. Geometridae), grasshoppers (Fam. Acrididae), and leafminers (Fam. Tineidae) are all relatively common on species of *Solanum*. No doubt there are many more. The smaller insects, e.g., flea beetles, can move readily between most prickles, and severe leaf damage on some very prickly species (by human standards), e.g., *S. prino-phyllum* Dunal, is evidence of this. In some cases dense prickles could conceivably keep large insects off the plant surface, but this must be quite rare and prickly species like *S. oedipus* Symon with well armed leaves and stems are extensively attacked by grasshoppers (pers. obs.). In looking through herbarium specimens I have concluded that apparent insect damage is more closely related to the length and density of the tomentum than to prickliness.

REPTILES

Although a few Australian reptiles (the larger Skinks) are herbivorous, their diet seems restricted to flowers and fruits. I have found none that regularly eat leaves of *Solanum* and they can be disregarded as significant herbivores of these species in Australia.

BIRDS

The two large flightless birds Emu and Cassowary are both herbivorous. The Cassowary is known to eat fruit (Stocker & Irvine, 1983), especially fallen fruit, and is not known to graze to any extent. Its distribution is strictly limited to rainforest areas of northern Queensland and it can scarcely be considered a significant factor in the more extensive browsing of plants.

By contrast, the Emu was extremely widespread and is omnivorous. Fruits, flowers, a wide range of vegetable matter, and insects make up its diet. It certainly eats *Solanum* fruits, even those with prickly calyces (Symon, 1979). Davies (1978) gave details of Emu diets in Western Australia. Within a very wide range of tolerance they take advantage of locally abundant fruit, flowers, herbage, and insects. Shoots and herbage formed an important part from January to October and grasses and Compositae shoots were ranked among the most abundant. The leaves of *S. ashbyae* were eaten in April and August. Davies did not list *Solanum* fruits in his tables or Appendices despite their importance in eastern Australia as cited by Noble (1975). Davies pointed out that Emus prefer succulent food items to dry ones, and such a diet does not include dried herbage or grasses or the mature leaves of shrubs. Three prickly plants provided significant amounts of food, i.e., *Acacia tetragonophylla*, *A. victoriae*, and *Scaevola spinescens*. In all cases the Emu ate the fruits and may be a dispersal agent rather than predator.

No native mammalian herbivores occurred in New Zealand and the only large vertebrates were the now extinct Moa. Greenwood and Atkinson (1977) suggested that the long-term effect of Moa browsing in New Zealand was the development of a large number of shrubs with an intricate divaricate growth habit, but scarcely any prickly shrubs. This thesis is challenged by McGlone and Webb (1981). The action of an Emu would be of plucking, pulling and breaking; the chewing or nibbling of an ungulate is scarcely possible. I have found no comment on the possible effect of Emus on the morphology of the Australian flora. A few intricate divaricate shrubs occur in Australia, but nowhere in the proportion that they occur in New Zealand. Their number could include *S. nummularium* S. Moore from Western Australia, of which the Emu would eat the ripe berries, rather than pluck the twigs. It is unlikely that the Emu is of significance as a browser of fresh foliage, although their role in seed dispersal is undoubted.

MAMMALS

In Australia mammalian herbivores would have been marsupials and to a lesser extent native rodents. No ungulates were originally native to Australia. The marsupials occur in great array ranging from kangaroos 2 m tall to the smallest wallabies, bandicoots, and possums, some no

larger than a rat, and these must be considered the major herbivores of the Australian flora. Some fossil species were larger than any living species and were considered to be browsers (Sanson, 1978). Because some of these became extinct in relatively recent times, it is likely their influence may still be reflected in the present vegetation.

Family Thylacomyidae, bandicoot. Watts (1969) in a paper on the distribution and habits of the rabbit-eared bandicoot (*Macrotis lagotis*) showed that plant material composed most of the diet and listed *Solanum* seed and *Solanum* roots as items of diet. *Solanum* seed remains in the feces formed 23% of the whole in one sample and in many cases were intact. Although once more widely spread, this bandicoot is now extremely restricted in number and area (an endangered species) and seems unlikely to have been an effective browser on *Solanum*.

Family Phalangeridae, possums. Van Dyck (1979) reported the destruction of wild tobacco tree (*S. mauritianum*) by mountain possums (*Trichosurus caninus*) in south east Queensland. This alien *Solanum* is a small tree, quite unarmed, and the animals ate the leaves and in particular the bark, often stripping the stems to ground level and causing their death. Van Dyck also gave other unpublished reports of the coppery brushtail (*T. vulpecula*) eating this species. Proctor-Gray (pers. comm.) reported that this species also eats the leaves and unripe fruits of *S. seaforthianum*, an unarmed, alien, climbing species. The native rainforest species of *Solanum* are rarely robust enough to sustain the weight of the possums, but their densely prickly main stems could reduce predation and protect the bark. Possums do not now occur over large areas of Australia, they are largely arboreal, and few *Solanum* in Australia are robust enough to sustain them. Freeland and Winter (1975) in a study of the brushtail possum (*T. vulpecula*) reported that this species spent up to 23% of its feeding time on the ground and that the animals "probably" ate the leaves of *S. nigrum* (?*S. americanum*), an unarmed species. Possums eat unarmed introduced *Solanum* but have not been reported eating prickly native species.

Family Petauridae, possums and gliders. No data located.

Family Macropodidae, kangaroos and wallabies. Sanson (1978), on the basis of mastication characteristics, divided the Macropodidae into a browsing grade and a grazing grade. The first was considered ancestral and included those

genera whose diet was substantially of soft, unabrasive, low fibre plant, whereas the latter was a derived grade specialised to eat the more abrasive, siliceous, high fibre grasses. The browsers included *Wallabia bicolor* (swamp wallaby), *Setonix brachyurus* (quokka), *Thylogale* spp. (pademelon), *Dendrolagus* spp. (tree kangaroo), *Lagostrophus* (hare wallaby), the New Guinea genera *Dorcopsis*, *Dorcopsulus*, and the extinct genera *Protemnodon*, *Hadronomas*, *Dorcopsoides*, and *Sthenurus*. An intermediate grade includes *Petrogale* (rock wallaby) and the fossil *Troposodon*.

The grazing grade included *Onychogalea* (nail-tail wallaby), *Lagorchestes* (hare wallaby), many, but not all of *Macropus*/*Megaleia* (kangaroo and euro), and the fossil *Peradorcas*, *Fissuridon*, and *Procoptodon*. In his (1978) paper, Sanson did not give specific names and the species included in his genus *Prionotemnus* are not stated. For this study and from Sanson (1980), I have considered *Macropus bernardus*, *M. fuliginosus*, *M. giganteus*, *M. parma*, *M. parryi*, *M. rufogriseus*, and *M. rufus* to be grazers and *Macropus agilis*, *M. dorsalis*, *M. eugenii* and *M. robustus* to be intermediate; *M. irma* is inadequately known and *M. greyi* is now extinct.

Sanson believed that the browsers did not consume large quantities of grasses, that extant browsers tend to show relict patterns of distribution, and that the oldest fossil members of the Macropodidae were all browsers. In contrast, the advanced grazers are distributed in recently developed arid and savannah grassland regions. Increasing aridity, the extinction of denser wet forests in the central regions of Australia, and an increase in grassland and shrub steppe at the end of the Miocene provided the impetus for change.

Bolton and Latz (1978) make no mention of *Solanum* in the brief list of plants eaten by the western hare-wallaby (*Lagorchestes hirsutus*). The diet given, though admittedly inadequate, suggests a grazer rather than a browser.

Christensen (1980), in a study of the woylie (*Beetongia penicillata*), showed that fungi composed a significant proportion of its diet throughout the year. Some starchy and cellular material was present but no mention was made of leafy herbage. No mention was made of *Solanum* in the diet or in the environment (likely to be rare in that area) and the woylie does not appear to be a significant herbivore of leafy material.

Stocker (1982) reported that the red-legged pademelon (*Thylogale stigmatica*) is active in stripping and eating the bark from the lower 50

cm of the alien *Solanum mauritianum* to the extent that the tops may be killed, though the base may coppice. This species is quite unarmed.

George (1982) stated that "the tree kangaroo (*Dendrolagus*) spends much of its time on the ground and presumably feeds predominantly on ground herbage." No precise details of its diet appear to be available.

Storr (1964) in a study of the quokka (*Setonix brachyurus*) on Rottnest Island, Western Australia recorded *Solanum simile* as a minor item of diet in January to March. The maximum percentage of the diet recorded comprising *Solanum* was 12%. This *Solanum* is quite unarmed. From the list of plants eaten it appears that the quokka is a browser rather than a grazer. Elsewhere Storr (1962) stated "the leaves, young stems and bark off older stems are only eaten in areas where little or no other herbage is available. Ripe fruits are eaten in summer and autumn. Ordinarily the plant is not important as food, it is more valuable as shelter when growing in dense thickets in burnt-out country." No prickly species of *Solanum* is listed for the island. *Solanum simile* belongs to the section *Archaeosolanum*, all species of which are unarmed. The section has significantly higher levels of solasodine alkaloids than do the stellate-haired prickly species.

Christensen (1980) reported on the stomach contents of the tammar (*Macropus eugenii*). In a thesis by Kelsall (1965) (not seen) it was stated that tammars browse predominantly on scrub species, particularly *Acacia* but are also attracted to grassy areas. An analysis by Christensen of the stomach contents of four animals disclosed 95, 90, 50% grassy material in three and 95% dicotyledonous material in the fourth. In contrast to *Bettongia*, very little fungal matter was present.

Maynes (1977) studied aspects of the biology of the parma wallaby, *Macropus parma*. This species is native to wet sclerophyll with a thick shrubby understory in association with grassy areas. Although observed to graze in grassy patches, no precise details of their diet were given.

Eight studies of the diet of the large red and grey kangaroos (*Macropus rufus* and *M. robustus*) were located (Chippendale, 1962; Kirkpatrick, 1965; Griffith & Barker, 1966; Chippendale, 1968; Storr, 1968; Bailey et al., 1971; Griffiths et al., 1974; Ellis et al., 1977).

These studies confirm that red kangaroos are essentially grass feeders and that browse is a mi-

nor component of their diet and neither can be considered as a major herbivore of *Solanum* although species of the latter occur wherever the larger kangaroos occur. The most prickly species of *Solanum* are not a feature of the plains where the larger grazing kangaroos occur.

Ealey and Main (1967) in a study of the ecology of the euro (*Macropus robustus*) in north-western Australia recorded a fruit of *Solanum lasiophyllum* in the mouth of one euro, but the genus was not otherwise recorded in their diet. However, Dawson and Ellis (1979) when comparing the diet of the euro and *Petrogale xanthopus* showed that though the euro showed a higher percentage of grass at all sampling times the component of plants with stellate trichomes was equally high in July 1974 and February 1978 and low in September 1976. It must therefore be considered as a herbivore of *Solanum*.

Dawson and Ellis (1979) compared the diet of *Petrogale xanthopus* (yellow-footed rock-wallaby) and sympatric herbivores in western New South Wales. The wallaby is now restricted in distribution in New South Wales and South Australia and occurs in rocky ranges. The plants with a tomentum of stellate hairs were classed together and included Solanaceae (*S. petrophilum*), Amaranthaceae, and Malvaceae. After three sampling periods the percentage of particles (plants with stellate trichomes) in the feces of the four animal species was wallaby 6–15%, euro 1–13%, goat 5–23%, rabbit 4–7%. The percentage of samples with stellate hairs was greatest in February 1978, "a notable component."

Copley and Robinson (1982) in their study of the diet of *Petrogale xanthopus* Gray (yellow-footed rock-wallaby) discussed six major dietary components of which one was plants with stellate trichomes (members of the families Solanaceae, Malvaceae, and Amaranthaceae), which could be recognised in the feces because of their characteristic stellate hairs. While this category constituted only about 5% of the diet in winter, it increased to 18–24% in summer (when species of these three plant families would be in active growth), and when fruits of *Solanum* were eaten as well evidenced by the seeds of *Solanum petrophilum* that occur in their feces. All the dietary components occurred in their highest proportion in close association with the rock outcrop. Although Copley and Robinson listed *S. petrophilum* and *S. sturtianum* as the species involved, both were common at the site. *Solanum petrophilum* was eaten throughout the year, in-

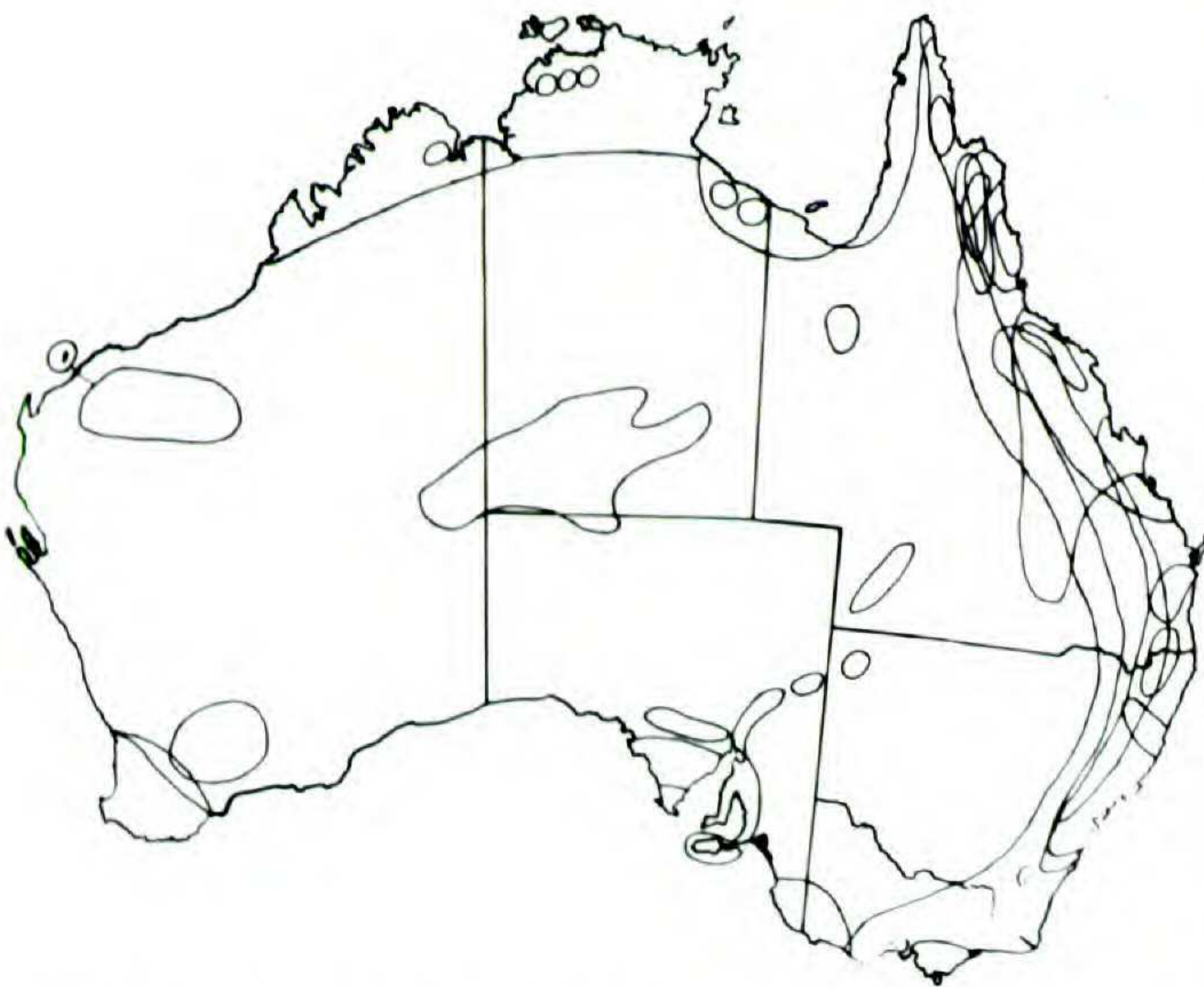


FIGURE 2. Distribution of the known browsing marsupials.

cluding flowers and fruit in spring and summer, and *S. sturtianum* was eaten in the summer.

Hornsby (pers. comm.) has shown me a videotape of a female yellow-footed rock wallaby in the Flinders Ranges eating the stems of *Solanum ellipticum*. The conditions were very dry at the time and the plants desiccated. The hands were used to break up the plant, after which the animal held pieces of the stem in its mouth and appeared to brush them vigorously with its hands to remove or break the prickles off before eating the remainder. The dried leaves did not appear to be eaten. Hornsby also reported then, that at other times of the year the animals selected and ate the flowers of *Solanum*. The bushes were carefully searched and only the flowers were eaten. *Eremophila* flowers were also selectively eaten. In experiments in October to November 1981, the animals were offered wilted and fresh material of *S. ellipticum*, *S. petrophilum*, and *S. sturtianum*. The flowers and fruits of *S. ellipticum* were eaten. Mature material of *S. sturtianum* was ignored but flowers were eaten. A joey showed distaste on sampling a leaf. The same joey later browsed some of the *S. ellipticum*. It is apparent from these studies that both the yellow-footed rock wallaby and the euro consume *Solanum* spp. and that particularly in summer *Solanum* may compose a measurable portion of their diet.

Short (1980) studied the ecology of the brush-tailed rock wallaby (*Petrogale penicillata*) at Kangaroo Valley (near Nowra) and Goulbourn River (near Muswellbrook) in New South Wales. Here grasses were a dominant element in the diet (33–50%), forbs (28–35%) and shrubs (12–30%)

together about equalled the grass. No *Solanum* was listed for the area or recorded in the diet. The intermediate position of *Petrogale* as both a grazer and browser was confirmed.

In a limited study of the swamp wallaby, *Wallabia bicolor*, Edwards and Ealey (1975) concluded that the species was a browser and that although the animals had access to grass and pasture these were scarcely eaten. The animals preferred coarse browse provided by shrubs and bushes. The swamp wallaby occurs in eastern Australia from Cape Yorke to Victoria and though *Solanum* was not mentioned in its diet or its environment, species occur in its area of occurrence. There is evidence that the browsing wallabies do eat prickly *Solanum*. For distribution of browsing marsupials see Figure 2.

Family Phascolarctidae, koala. The koala (*Phascolarctos cinereus*) eats *Eucalyptus* only and is very specialised in its choice of species. It need not be considered in this context as a browsing herbivore.

Family Vombatidae, wombats. The few species are grazers, not browsing herbivores and feed principally on monocotyledons (Wells, pers. comm.).

Family Tarsipedidae, honey possums. Although herbivorous, this species has a specialised diet of pollen, nectar, and fruit and is not a browsing herbivore.

Rodents. Three studies of the diets of Australian rodents (Watts, 1970, 1977; Watts & Braithwaite, 1978) record *Solanum* seed as a minor element of the diet of *Notomys alexis* at Yuendumu (Northern Territory) and there is no other mention of *Solanum*.

P. P. M. Hyland and B. Gray (pers. comm., 1981) stated that rats are known to eat the bark of *S. mauritianum* and *S. torvum*. Both these are alien weedy species that occur in wet tropical areas in eastern Australia. The first is unarmed, the second is prickly. Though possibly significant locally or when in plague numbers there is no evidence to suggest rodents are important as grazers.

THE RESPONSE OF *SOLANUM* IN THE ABSENCE OF HERBIVORES

Hawaii has always been an oceanic island and originally had a very limited vertebrate fauna. The nucleus of the whole flora arrived by long distance dispersal and has since speciated richly. There are about six native species of *Solanum* (St. John, 1973); of these, five are unarmed and

only one, *S. haleakalaense*, is well armed. This last species may have been a late arrival that has not yet lost its prickles or the prickles may deter snails, which are abundant in Hawaii. I have not seen it growing in the field. Carlquist (1970) discussed the prickles on some of the lobelioids in Hawaii. The family Campanulaceae subfamily Lobelioideae is not noted for the development of prickles. The plants are often acrid, bitter, and unpalatable, and many contain indole alkaloids. In Hawaii many species are densely prickly in the young stages and may even have prickly inflorescences and flowers. Carlquist considered this a defense against snails because no other herbivores are well developed in Hawaii. It is possible, although I have no evidence to support it, that the Australian species of *Solanum* with extremely dense stem prickles that grow in the high rainfall sites, such as *S. macoorai*, *S. oedipus*, and *S. semiarmatum*, may also be protected against snails.

Fiji, without mammalian herbivores, has six species of *Solanum*, probably native, all of which are unarmed, including *S. repandum* Forster, whose close relatives in South East Asia and South America are prickly (Whalen et al., 1981). New Caledonia also lacked mammalian herbivores. Heine (1976) listed 10 native species, of which seven are unarmed and three have traces of prickles. Included in these three is *S. vaccinioides*, which varies from being unarmed to having prickles present, as might be expected if the original immigrant was prickly and the selection pressure for prickles was relaxed.

Tomlinson (1962) discussed the pungency of palms that may develop prickles from leaves, stem emergences, or the roots. He suggested that their role is defence of the single large apical bud and that there are now few large animals capable of tearing open the heart of the palm. Without discussing it further he pointed out that many unarmed palms occur on the isolated islands of the Pacific, where there are few or small vertebrate animals.

These examples support the thesis that prickles are primarily a response to herbivory and have little relationship to the physical environment.

THE EFFECT OF EXTINCT MARSUPIALS

The extinct marsupials, some of which were very large, must have had some effect on the vegetation and in some cases may have acted as seed dispersal agents. Some of these animals survived to the late Pleistocene and certainly over-

lapped the arrival of aboriginal man in Australia. Sanson (1978) considered most of the extinct macropodids to be browsers. Many of the others were herbivores, e.g., diprotodontids, phascolarctids, palorchestids, and vombatids, and included both browsers and grazers (Archer, 1981). Janzen (1982) claimed to detect a suite of Central American plants whose fruits were probably dispersed by the recently extinct large herbivores of that area. A parallel in Australia is not immediately obvious, but the influence of the browsers on some of the remaining vegetation, particularly in those areas now occupied by the grazing kangaroos, might be worth searching for.

CONCLUSION

The evidence assembled suggests that prickles on *Solanum* are not an adaptation to aridity. The scattered and incomplete records of the diet of Australian vertebrate herbivores suggests that the relic group of marsupials called wallabies and prickly *Solanum* do in general coincide. The distribution of wallabies may have contracted in geologically recent times due to increasing aridity but prickly *Solanum* still remain in some areas where wallabies are now extinct.

LITERATURE CITED

- ALLAN, H. H. 1961. Flora of New Zealand. Gov. Printer Wellington, New Zealand.
- ARCHER, M. 1981. A review of the origins and radiations of Australian mammals. In A. Keast (editor), Ecological Biogeography of Australia. Monographie Biologie 41: 1437–1488. Dr. W. Junk, The Hague.
- BAILEY, P. T., P. N. MATENZ & R. BARKER. 1971. The red kangaroo *Megaleia rufa* (Desmarest) in north-western New South Wales 11. Food. CSIRO Wildl. Res. 16: 29–39.
- BOLTON, B. L. & P. K. LATZ. 1978. The western hare-wallaby *Lagorchestes hirsutus* (Gould) (Macropodidae) in the Tanami Desert. Austral. Wildl. Res. 5: 285–293.
- BRADLEY, V., D. J. COLLINS, P. G. CRABBE, F. W. EASTWOOD, M. C. IRVINE, J. M. SWAN & D. E. SYMON. 1978. A survey of Australian *Solanum* plants for potentially useful sources of Solasadine. Austral. J. Bot. 26: 723–754.
- CARLQUIST, S. 1970. Hawaii: A Natural History. Nat. Hist. Press, New York.
- CHIPPENDALE, G. M. 1962. Botanical examination of kangaroo stomach contents and cattle rumen contents. Austral. J. Sci. 25: 21–22.
- . 1968. The plants grazed by red kangaroos *Megaleia rufa* (Desmarest) in Central Australia. Proc. Linn. Soc. New South Wales 93: 98–110.
- CHRISTENSEN, P. E. S. 1980. The biology of *Bettongia penicillata* (Gray, 1837) and *Macropus eugenii* (Desmarest 1817) in relation to fire. Forests Dept. W. Aust. Bull. 91.

- COPLEY, P. G. 1982. Studies of the yellow-footed rock wallaby, *Petrogale xanthopus*. I. Distribution in South Australia. *Austral. Wild. Res.* 10: 47–61.
- & A. C. ROBINSON. 1982. Studies of the yellow-footed rock wallaby, *Petrogale xanthopus* Gray (Marsupialia, Macropodidae) II. Diet. *Austral. Wild. Res.* 10: 63–76.
- DAVIES, S. J. J. F. 1978. The food of emus. *Aust. J. Ecol.* 3: 411–422.
- DAVIS, P. H. & V. H. HEYWOOD. 1967. *Principles of Angiosperm Taxonomy*. Oliver & Boyd, Edinburgh.
- DAWSON, T. J. & B. A. ELLIS. 1979. Comparison of the diets of yellow-footed rock-wallabies and sympatric herbivores in Western New South Wales. *Austral. Wild. Res.* 6: 245–254.
- EALEY, E. H. M. & A. R. MAIN. 1967. Ecology of the euro, *Macropus robustus* (Gould) in north-western Australia. *CSIRO Wildl. Res.* 12: 53–65.
- EDWARDS, G. P. & E. H. M. EALEY. 1975. Aspects of the ecology of the swamp wallaby *Wallabia bicolor* (Marsupialia: Macropodidae). *Australian Mammalogy* 1: 307–317.
- ELLIS, B. A., E. M. RUSSELL, T. J. DAWSON & C. J. F. HARROP. 1977. Seasonal changes in diet preferences of free-ranging red kangaroos, euros & sheep in Western New South Wales. *Austral. Wild. Res.* 4: 127–144.
- FREELAND, W. J. & J. W. WINTER. 1975. The evolutionary consequences of eating: *Trichosurus vulpecula* (Marsupialia) and the genus *Eucalyptus*. *J. Chem. Ecol.* 1: 439–455.
- FRITSCH, F. E. & E. SALISBURY. 1953. *Plant Form and Function*. Bell, London.
- GREENWOOD, R. M. & I. A. E. ATKINSON. 1977. Evolution of divaricating plants in New Zealand in relation to Moa browsing. *Proc. New Zealand Ecol. Soc.* 24: 21–33.
- GRIFFITHS, M. & R. BARKER. 1966. The plants eaten by sheep and kangaroos grazing together in a paddock in south-western Queensland. *CSIRO Wildl. Res.* 11: 145–162.
- , ——— & L. MCLEAN. 1974. Further observations on the plants eaten by kangaroos and sheep grazing together in a paddock in south-western Queensland. *Austral. Wild. Res.* 1: 27–43.
- HEINE, H. 1976. Flore de la Nouvelle Calédonie et dépendances. *Mus. Nat. d'Hist. Nat. Paris* 7: 119–212.
- JANZEN, D. H. 1981. The defenses of legumes against herbivores. In R. M. Polhill & P. H. Raven (editors), *H.M.S.O., Advances in Legume Systematics* 2: 951–977.
- . 1982. Neotropical anachronisms: the fruits the Gomphotheres ate. *Science* 215: 19–27.
- KERNER, A. 1895. *The Natural History of Plants*. Oliver translation. Blackie & Son, London.
- KIRKPATRICK, T. H. 1965. Food preferences of the grey kangaroo (*Macropus major* Shaw). *Queensland J. Agric. Sci.* 22: 89–93.
- MAIN, A. R. 1981. Plants as animal food. In J. S. Pate & A. J. McComb (editors), *The Biology of Australian Plants*. University of Western Australia Press.
- MAYNES, G. M. 1977. Distribution and aspects of the biology of Parma Wallaby *Macropus parma* in New South Wales. *Austral. Wild. Res.* 4: 109–125.
- MCGLOONE, M. S. & C. J. WEBB. 1981. Selective forces influencing the evolution of divaricating plants. *New Zealand J. Ecol.* 4: 20–28.
- NOBLE, J. C. 1975. Difference in size of Emus on two contrasting diets on the riverine plain of New South Wales. *The Emu* 75: 35–37.
- SANSON, G. D. 1978. The evolution and significance of mastication in the Macropodidae. *Australian Mammalogy* 2: 23–28.
- . 1980. The morphology and occlusion of the molariform cheek teeth in some Macropodinae (Marsupialia: Macropodidae). *Austral. J. Zool.* 28: 341–365.
- SEITHE, A. 1979. Hair types as taxonomic characters in *Solanum*. Pp. 307–319 in J. G. Hawkes, R. N. Lester & A. D. Skelding (editors), *The Biology and Taxonomy of the Solanaceae*. Academic Press, London.
- SHORT, J. C. 1980. Ecology of the Brush Tailed Rock Wallaby (*Petrogale penicillata* Griffith, Smith & Pidgeon). M.Sc. Thesis. Univ. of Sydney.
- ST. JOHN, H. 1973. List of flowering plants in Hawaii. *Pacific Trop. Bot. Gard. Mem.* 1: 300–301.
- STOCKER, G. C. & A. K. IRVINE. 1983. Seed dispersal by Cassowaries (*Casuarius casuarius* L.) in the north Queensland rain forests. *Biotropica* 15: 170–176.
- STORR, G. M. 1962. Annotated flora of Rottnest Island Western Australia. *West. Austral. Nat.* 8: 109–124.
- . 1964. Diet of the Quokka *Setonix brachyurus* (Quoy & Gaimard), on Rottnest Island, Western Australia. *Austral. J. Biol. Sci.* 17: 469–481.
- . 1968. Diet of kangaroos *Megaleia rufa* and *Macropus robustus* and merino sheep near Port Hedland, Western Australia. *J. & Proc. Roy. Soc. Western Australia* 51: 25–32.
- SYMON, D. 1979. Fruit diversity and dispersal in *Solanum* in Australia. *J. Adelaide Bot. Gard.* 1: 321–331.
- . 1981. A revision of the genus *Solanum* in Australia. *J. Adelaide Bot. Gard.* 4: 1–367.
- TOMLINSON, P. B. 1962. Essays on the morphology of palms. VII. A digression about spines. *Principes* 6: 44–52.
- VAN DYCK, S. 1979. Destruction of wild tobacco trees (*Solanum mauritianum*) by mountain possums (*Trichosurus caninus*). *Mem. Queensland Mus.* 19: 367–371.
- WATTS, C. H. S. 1969. Distribution and habits of the rabbit bandicoot. *Trans. & Proc. Roy. Soc. South Australia* 93: 135–141.
- . 1970. The foods eaten by some Australian desert rodents. *S. Austral. Naturalist* 44: 71–74.
- . 1977. The foods eaten by some Australian rodents (Muridae). *Austral. Wild. Res.* 4: 151–157.
- & R. W. BRAITHWAITE. 1978. The diet of *Rattus lutreolus* and five other rodents in Southern Victoria. *Austral. Wild. Res.* 5: 47–57.
- WHALEN, M. D., D. E. COSTICH & C. B. HEISER. 1981. Taxonomy of *Solanum* section *Lasiocarpa*. *Gentes Herb.* 12: 41–129.